
Faculty of Social Science

Faculty Publications

Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models

Joanna M. Burgar, Frances E.C. Stewart, John P. Volpe, Jason T. Fisher, A. Cole Burton

2018

© 2018 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

This article was originally published at:

<https://doi.org/10.1016/j.gecco.2018.e00411>

Citation for this paper:

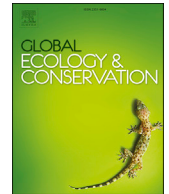
Burgar, J.M., Stewart, F.E.C., Volpe, J.P., Fisher, J.T. & Burton, A.C. (2018). Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models. *Global Ecology and Conservation*, 15, e00411. <https://doi.org/10.1016/j.gecco.2018.e00411>



ELSEVIER

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: <http://www.elsevier.com/locate/gecco>

Original Research Article

Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models

Joanna M. Burgar^{a, b, *}, Frances E.C. Stewart^b, John P. Volpe^b, Jason T. Fisher^{b, c},
A. Cole Burton^a

^a University of British Columbia, Department of Forest Resources Management, 2424 Main Mall, Vancouver, V6T 1Z4, Canada

^b University of Victoria, School of Environmental Studies, 3800 Finnerty Rd., Victoria, V8W 2Y2, Canada

^c Ecosystem Management Unit, InnoTech Alberta, 3-4476 Markham St, Victoria, V8Z 7X8, BC, Canada

ARTICLE INFO

Article history:

Received 3 March 2018

Received in revised form 29 May 2018

Accepted 3 July 2018

Keywords:

Bayesian estimation

Camera trap surveys

Cost-effectiveness

Non-invasive genetic sampling

Pekania pennanti

Population monitoring

Wildlife conservation

ABSTRACT

Density estimation is integral to the effective conservation and management of wildlife. Camera traps in conjunction with spatial capture-recapture (SCR) models have been used to accurately and precisely estimate densities of “marked” wildlife populations comprising identifiable individuals. The emergence of spatial count (SC) models holds promise for cost-effective density estimation of “unmarked” wildlife populations when individuals are not identifiable. We evaluated model agreement, precision, and survey costs, between i) a fully marked approach using SCR models fit using non-invasive genetic data, and ii) an unmarked approach using SC models fit using camera trap data, for a recovering population of the mesocarnivore fisher (*Pekania pennanti*). The SCR density estimates ranged from 2.95 to 3.42 (2.18–5.19 95% BCI) fishers 100 km⁻². The SC density estimates were influenced by their priors, ranging from 0.95 (0.65–2.95 95% BCI) fishers 100 km⁻² for the uninformative model to 3.60 (2.01–7.55 95% BCI) fishers 100 km⁻² for the model informed by prior knowledge of a 16 km² fisher home range. We caution against using strongly informative priors but instead recommend using a range of unweighted prior knowledge. Thin detection data was problematic for both SCR and SC models, potentially producing biased low estimates. The total cost of the genetic survey (\$47 610) was two-thirds of the camera trap survey (\$77 080), or comparable (\$75 746) if genetic sampling effort was increased to include sex and trap-behaviour covariates in SCR models. Density estimation of unmarked populations continues to be a series of trade-offs but as methods improve and integrate, so will our estimates.

© 2018 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Estimating the density of animals is integral to researching, conserving, and managing wildlife populations (Williams et al., 2002). Population data are imperative for applying appropriate and effective conservation interventions, such as deciding when and where to focus protection efforts for threatened species (Bradley et al., 2017), delineating sustainable

* Corresponding author. University of British Columbia, Department of Forest Resources Management, 2424 Main Mall, Vancouver, V6T 1Z4, Canada.
E-mail address: joburgar@gmail.com (J.M. Burgar).

harvest levels (Kachel et al., 2016), or mitigating human-wildlife conflict (Mcgregor et al., 2015). Effective conservation management requires that density estimates are both accurate and precise, and produced with sufficient frequency to ensure informed decision-making (Jiménez et al., 2017). This is especially true for species of conservation concern where inaccurate and imprecise estimates can provide a false signal of stability (Tobler and Powell, 2013) and result in a lack of needed conservation effort (Bauer et al., 2015).

The past decade has seen parallel and complementary developments in field and statistical density estimation methods. There has been a move away from labour-intensive and invasive field surveys to the use of non-invasive remote sensing devices, such as camera traps (e.g., Burton et al., 2015). At the same time, analyses are shifting from traditional (e.g., capture-recapture models) to more complex statistical techniques, such as spatial capture-recapture (SCR) models (Borchers and Efford, 2008; Efford, 2004; Royle and Young, 2008). SCR models are an extension of traditional capture-recapture models that explicitly account for trap location and animal movement. They have been widely applied to field data, predominantly to estimate mammalian (carnivore) density (e.g., Royle et al., 2011) but also for birds (Mollet et al., 2015), sharks (Bradley et al., 2017), amphibians (Muñoz et al., 2016), and insects (Torres-Vila et al., 2012). The majority of SCR models are applied to camera trap survey data of naturally marked individuals (e.g., Avgan et al., 2014), secondly to data generated from genetic sampling methods (e.g., Gardner et al., 2010), and less frequently to other data types, such as acoustic recordings (Dawson and Efford, 2009). With the advancement of both field and analytical methods, density estimates are now being produced for previously unstudied populations (e.g., Sollmann et al., 2014). While SCR models are proving extremely useful for estimating the density of uniquely identifiable individuals — e.g., unique pelage markings or genetic analysis of hair and scat samples — many species are not uniquely identifiable from camera trap images, and other means of individual identification may be prohibitively costly or invasive.

The global increase in camera trap surveys has generated large volumes of data on a broad range of species (Steenweg et al., 2017), raising the possibility of simultaneously monitoring multiple species, including those that were not the original focus of the study (Rayan et al., 2012; Scotson et al., 2017). Indeed, 60% of camera trap studies comprise multiple species surveys (Burton et al., 2015), potentially representing a wealth of data available for species density estimation if models could reliably estimate densities of unmarked populations. Based on the results of previous simulation studies, spatial mark-resight (SMR) and spatial count (SC) models show great promise for estimating densities of populations where some or all individuals within the population are unmarked (Chandler and Royle, 2013). However, few published papers apply these models to field data (Evans et al., 2017; Jiménez et al., 2017; Kane et al., 2015; Rich et al., 2014; Sollmann et al., 2013), and when applied, SMR and SC models do not always converge (e.g., Sollmann et al., 2013). As conservation scientists and practitioners begin to use these more advanced models, there is a need to further assess their potential for producing reliable estimates from empirical datasets.

In this study, we capitalized on data collected as part of a study on the genetics and landscape connectivity of a recovering population of the mesocarnivore fisher (*Pekania pennanti*) (Stewart et al., 2017). Previous research on fishers in other regions includes estimates of density and home range size (e.g., Fuller et al., 2001; Koen et al., 2007; Linden et al., 2017), making it a useful species with which to compare SCR and SC models for conservation objectives. Our study goals were threefold: 1) estimate fisher density from an SCR model using non-invasive genetic survey data; 2) evaluate the ability of an SC model using concurrent camera trap survey data to produce comparable estimates; and 3) compare the costs and benefits associated with both sampling methods.

Our study builds on a recent fisher population study that compared density estimates using individual genetic data in a SCR model to camera detection data in a Royle-Nichols model (Linden et al., 2017). The unmarked modelling approach that we evaluate (SC) explicitly uses the spatial correlation of count data to estimate density (Chandler and Royle, 2013), in contrast to the Royle-Nichols model, which assumes that individuals are counted only once per sampling occasion (Royle, 2004), a condition violated in our survey. We include a cost comparison of methods as managers and conservationists must routinely weigh the benefits of a sampling approach against the feasibility, including costs, of implementation. Thus, our goal was to evaluate the analytical component while considering field costs, as conservation practitioners rarely consider one without the other when designing a monitoring program. We recognize that the type of survey is dictated by the research question; it is not our intention to discourage the use of either genetic or camera trap surveys. Rather, our analyses provide guidance on the advantages and limitations of using these field and statistical methods for estimating population density and informing conservation decisions.

2. Materials and methods

2.1. Study area and sampling design

Our study took place on the Cooking Lake Moraine (53.381 °N, 113.063 °W), a multi-use landscape of exurban development, protected areas, and agriculture covering 1596 km² in central Alberta, Canada (Fig. 1). The forested sections of this landscape were dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), with clusters of white and black spruce (*Picea glauca* and *P. mariana*) interspersed with small water bodies characteristic of a glacial moraine. A diverse mammal community occupied this heterogeneous landscape, including fisher, a medium sized mustelid (2.2–7.0 kg) native to North American forests (Powell, 1982; Stewart et al., 2018).

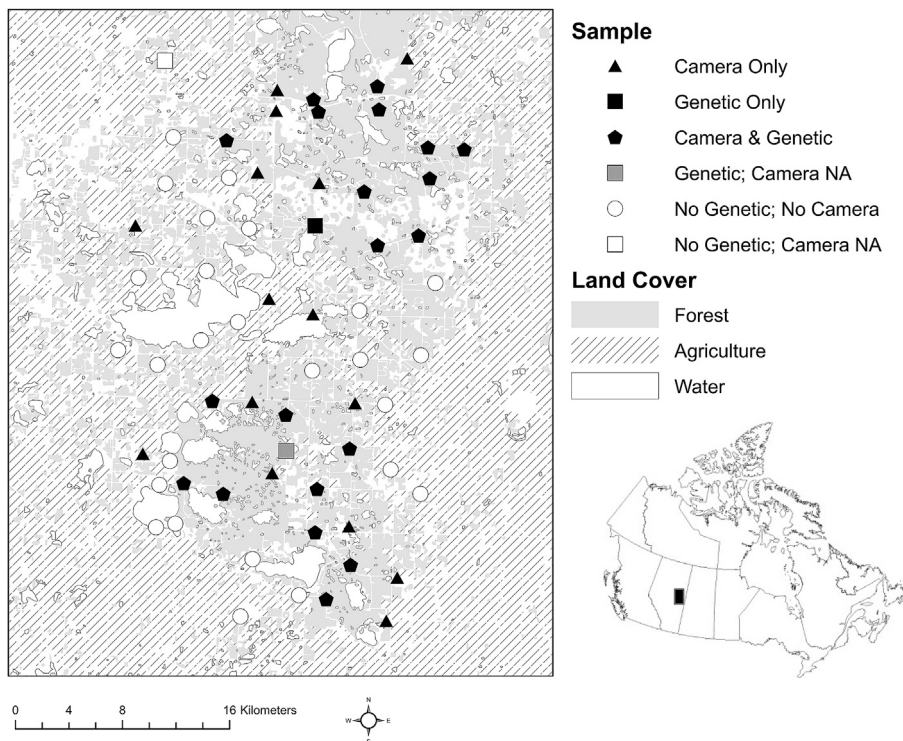


Fig. 1. The study area encompassed 64 fisher sampling sites, each within one $4 \times 4 \text{ km}^2$ grid cell, in the Cooking Lake Moraine (Alberta, Canada). Genetic samples were collected from 64 site hair traps (January to April 2016) while images were collected from 62 site camera traps (1 January to 4 March 2016). The symbols refer to fisher detections by sampling type at each site; NA indicates the sites where cameras were inactive.

Fisher density was surveyed using a multi-method approach (sensu Fisher and Bradbury, 2014) combining non-invasive genetic tagging via hair sampling and infra-red remote cameras. The study area comprised 64 grid cells deployed in a systematic sampling design (Fig. 1), each $4 \times 4 \text{ km}^2$ to approximate fisher home range (Linden et al., 2017). Within each cell a sampling site was composed of a hair trap, consisting of a tree wrapped in barbed wire and baited with $\sim 5 \text{ kg}$ of beaver carcass and a commercial scent lure (O’Gorman’s™ Long Distance Call), and a Reconyx PC900 Hyperfire™ infra-red remote digital camera. To meet the assumption of a closed population we sampled during a period of localized movement, rather than dispersal, from January to April 2016 (Powell, 1982). Hair traps were checked monthly to maximize detections between site visits while minimizing DNA degradation due to exposure (Foran et al., 1997): checks involved DNA sample collection and torching the barb wire to avoid contamination between monthly DNA samples. DNA was extracted from collected hairs and analyzed to identify species, individual, and sex using 15 microsatellite primers (Appendix A; Stewart et al., 2017).

Cameras were placed $\sim 6\text{--}10 \text{ m}$ away from, and facing, the baited tree, and were $\sim 1.5 \text{ m}$ above the ground; the camera’s field of view included the hair trap, bait, and surrounding area. Cameras were triggered by heat-in-motion and recorded five consecutive photographs with 1 s delay between each. There was no set delay between detection events. We subset the camera data to the period when the maximum number of cameras were continuously operational; the final camera detection dataset comprised 62 sites operating for 64 days from January 1 to March 4, 2016. For the camera data, fisher detection events were considered independent when the time between subsequent fisher images was $>60 \text{ min}$. There were only slightly fewer detection events with a 60-min threshold than if we set a 30-min threshold, and no difference from 120- or 180-min thresholds. Research was permitted by Alberta Environment and Parks (16-004) and University of Alberta Animal Care Committee (AUP00000518).

2.2. Model implementation

We compared Bayesian spatial capture-recapture (SCR) models fit using the genetic data (Royle et al., 2014) with Bayesian spatial count (SC) models fit using the camera data (Chandler and Royle, 2013). SCR models are an extension of traditional capture-recapture models in that they explicitly incorporate spatial information, rather than ignoring that information or treating it as a nuisance variable as done in traditional capture-recapture models (Efford, 2004; Royle et al., 2014). SCR models consider N individuals to be located within a state-space S during the survey period. S theoretically encompasses all traps as well as a surrounding area large enough to contain all individuals that may have been exposed to the survey. Each individual has an activity centre within S , analogous to the individual’s home range centre during the study period. The population is

sampled at J traps over K occasions, with encounters by n individuals. An individual's probability of encounter p_{ij} is conditional on where individual i lives. If we define an individual's activity centre as a two-dimensional spatial coordinate \mathbf{s}_i , then p_{ij} can be expressed as a decreasing function of the Euclidean distance between \mathbf{s}_i and the location of trap j (Royle et al., 2014). We defined the baseline encounter probability as λ_0 .

For the SCR models, hair samples were collected once a month with one genetic sample identified per trap; thus detections effectively followed a binomial distribution with an individual either being present or absent at each trap on each sampling occasion. For the SC models individuals were not known, but inferred, and we assumed that these latent encounter histories for individual i at trap j during sample occasion k , y_{ijk} , were mutually independent outcomes of a Poisson random variable, which expresses the probability of a given number of events occurring in a fixed interval of time and space. Both SCR and SC models also estimate σ , a spatial scale parameter determining the rate at which the encounter probability declines with distance.

The Bayesian approach to SCR modelling requires data augmentation, i.e., setting the population at some augmented size M by adding potential unobserved individuals with an all-zero encounter history to create a dataset with a zero-inflated population (Royle and Dorazio, 2012; Royle and Young, 2008). N is a derived variable, the product of M and ψ : the proportion of individuals within the augmented population that occur within the sampled population. Density, D , can then be calculated by dividing N by S . The difference between SC and SCR models is that SC models deal with unidentified individuals by using spatial correlations in observed counts to infer the locations of individual activity centres (Chandler and Royle, 2013; Royle et al., 2014). Formulating SC models requires combining random effects for individual identity with the random effect of locations of individual activity centres (Appendix B).

As space use and site fidelity can differ between sexes, and baiting traps has been shown to produce a positive trap-behaviour response in fishers (Linden et al., 2017) we included a sex effect and a trap-behaviour response in our SCR model. However, adding covariates can reduce precision, especially for elusive carnivores with low detection rates, thus we also ran "base" SCR models without covariates (all models described in Appendix B). In all models we set M to 300, well above the expected population size. We ran models using JAGS (Plummer, 2003), interfacing through R using the *jagsUI* (Kellner, 2016) and the *rjags* (Plummer, 2016) packages for the SCR and SC models, respectively. We ran one model with uninformative priors while the remaining three had informative σ priors. For the uninformative models we specified the σ prior with a uniform distribution between 0 and 1000. For the informative models we considered fisher home range sizes from the literature (16 km²; Linden et al., 2017) and a concurrent telemetry study (4–72 km²; Appendix C). For the first informative σ prior we allowed for a wide range of home range estimates (4–72 km²), while not adding weight to any particular home range size. The other two informative σ priors were defined by designating cumulative prior distribution weight to home range estimates of 16 km² and 40 km², respectively. We used gamma distributions to specify these priors, following Chandler and Royle (2013; Table C1). For all models we specified a λ_0 prior with a uniform distribution between 0 and 10 and a ψ prior with a beta distribution having shape and scale set to 1. For the SCR models we ran three chains for 12 000 iterations with a burn in of 2000 (after an adaptive phase of 100). For the SC models we ran three chains for 100 000 iterations with a burn in of 50 000 (after an adaptive phase of 1000). We did not thin the posterior distributions. Model output was viewed using the package *coda* (Plummer et al., 2006). For all models we added a buffer of 4 km (>3 times our calculated sigma for a home range of 40 km²) to the outermost trap coordinates for a state-space of 1695 km².

2.3. Survey method cost comparison

We calculated the cost associated with each survey method, including the field equipment and logistics, sample processing, and analysis. It took two people one hour to initially set up each site and 10 person-days month⁻¹ to service the 64 sites. The two-month camera trap study required a total of 172.8 person-hours for initial set-up, servicing half way through to re-bait, and retrieval. The four-month genetic survey required an investment of 262.4 person-hours across five site visits: initial set up, three visits to sample for hair and re-bait, and a final visit to sample and retrieve equipment. For comparison purposes we assumed each survey was conducted independently and calculated costs as such, although in reality costs were shared between surveys for the first three site visits. Genetic samples were sent to Wildlife Genetics International (Nelson, BC, Canada) for DNA microsatellite analysis whereas camera image processing and statistical analyses were conducted by the authors (FECS and JMB, respectively). Field, image processing, and statistical analysis labour costs were set to \$20 hr⁻¹ for consistency. This study used high-quality remote camera equipment; to make the comparison more generalizable we provide expected low and medium equipment costs in Appendix D.

3. Results

3.1. Fisher detections

We collected 146 hair samples, of which 103 were identified as fisher but only 43 yielded sufficient genetic data to identify individuals (42% overall success rate). Five females and five males were detected more than once, up to three times per individual female and up to seven times per individual male. Microsatellite analyses identified 24 individual fishers (Appendix A; Stewart et al., 2017): 15 females and nine males, for a total of 21 female and 22 male genetic fisher detections over the four, month-long sampling occasions. The mean maximum distance between recaptures was 6.0 km. For the camera data, there

were 169 independent fisher detection events across 62 sites over the 64, day-long sampling occasions. The detection rate [# detections]/[# traps * # sampling occasions] was higher for the genetic survey (17%) compared to the camera trap survey (4%) despite fishers being detected at 33 camera traps (53%) versus 19 hair traps (31%; Fig. 1). During the period when both types of traps were operating concurrently, fishers were detected by cameras at 15 sites where they were not detected by hair traps, whereas all hair trap detections were also detected by cameras.

3.2. Model performance

For all models, the Brooks and Gelman (1998) multivariate potential scale reduction factor was ≤ 1.02 and the potential scale reduction factors for individual parameters were all ≤ 1.06 . These values, along with visual inspection of the trace plots for each parameter, indicated convergence of the MCMC chains on each run. The 95% Bayesian credible intervals (BCI) of the full SCR model density estimates were 4–5 times wider than the BCI of the base SCR model; as such, estimates of the full SCR model are only reported in the Appendix (Table E1). We focus our results on the comparison of the base SCR model (without covariates) to the SC model. The estimated population was well below the data augmented population, with $\Psi \leq 0.31$ and 0.43 for the SCR and SC models, respectively (Table 1).

3.3. Density estimation

Density estimates varied among methods and model structures (Table 1, Fig. 2). The SCR density estimates were similar regardless of the prior on σ , estimating between 2.95 and 3.42 fishers 100 km^{-2} with 95% BCI ranging from 2.18 to 5.19 fishers 100 km^{-2} . In contrast, density estimates from the SC models were influenced by their σ priors. They ranged from 0.95 (0.65–2.95 95% BCI) fishers 100 km^{-2} for the uninformative model to 3.60 (2.01–7.55 95% BCI) fishers 100 km^{-2} for the σ prior equating to a home range size of 16 km^2 , the only SC estimate that did not underestimate density compared to the SCR estimates. The SC model with the unweighted informative σ prior, representing the range of home range sizes calculated from the concurrent telemetry study, estimated 1.5 (0.73–3.91 95% BCI) fishers 100 km^{-2} .

Unsurprisingly, the prior on σ influenced the σ estimates, particularly for the SC models (Table 1, Fig. 3). The uninformative models produced the largest σ estimates, which were 2.48 km for the SCR model: (1.98–3.45 95% BCI); and 1.80 km for the SC model (1.40–2.67 95% BCI). The models with the σ prior equating to a home range size of 16 km^2 produced the smallest σ estimates [SCR: 1.62 (1.45–1.87 95% BCI) km; SC: 1.07 (0.84–1.44 95% BCI) km]. The σ estimates from the unweighted informative σ prior model were 96 km^2 and 55 km^2 for the SCR and SC models, respectively. SC λ_0 estimates were consistently low (0.13–0.14) while the SCR λ_0 estimates doubled for models with weighted σ priors (up to 0.35; Table 1). Coefficient of variation (CV; standard deviation divided by the mean) values for density, σ and λ_0 were between 6–35% and 9–52% for the SCR and SC models, respectively (Table 1).

3.4. Surveys costs

The total cost of our genetic survey (\$47 610) was two-thirds that of the camera trap survey (\$77 080), despite the genetic survey requiring two additional visits per site (Table D1). The additional expense for the camera trap survey was due to initial capital costs in purchasing the camera equipment. Using less expensive camera traps would drastically reduce survey costs (Appendix D), although this may reduce data quality, particularly when less expensive equipment is used for multiple years (Newey et al., 2015). Assuming equipment would be reused, subsequent surveys would cost moderately less for genetic

Table 1

Spatial capture-recapture (SCR) and spatial count (SC) posterior summaries for fishers sampled in the Cooking Lake Moraine from January to April, 2016. Parameter values are presented as the mode with 95% Bayesian credible intervals and coefficient of variation (CV; standard deviation divided by the mean * 100).

	Uninformative σ		Informative σ ($4\text{--}72 \text{ km}^2$)		Informative σ (16 km^2)		Informative σ (40 km^2)	
	SCR	SC	SCR	SC	SCR	SC	SCR	SC
D^a	2.95 (2.18, 4.72)	0.95 (0.65, 2.95)	3.25 (2.18, 4.84)	1.51 (0.73, 3.91)	3.42 (2.36, 5.19)	3.60 (2.01, 7.55)	3.42 (2.30, 5.02)	1.56 (1.03, 3.37)
$D \text{ CV}$	22%	43%	21%	52%	20%	34%	21%	31%
λ_0^b	0.15 (0.07, 0.28)	0.13 (0.08, 0.21)	0.17 (0.09, 0.34)	0.13 (0.08, 0.21)	0.35 (0.19, 0.75)	0.14 (0.09, 0.22)	0.25 (0.14, 0.49)	0.14 (0.09, 0.22)
$\lambda_0 \text{ CV}$	19%	23%	20%	23%	35%	23%	24%	25%
σ^c	2.48 (1.98, 3.45)	1.80 (1.40, 2.67)	2.26 (1.85, 2.90)	1.71 (1.19, 2.35)	1.62 (1.45, 1.87)	1.07 (0.84, 1.44)	1.91 (1.66, 2.18)	1.63 (1.34, 1.92)
$\sigma \text{ CV}$	15%	17%	12%	16%	6%	14%	7%	9%
Ψ^d	0.18 (0.11, 0.28)	0.06 (0.03, 0.18)	0.18 (0.11, 0.29)	0.09 (0.05, 0.27)	0.19 (0.12, 0.31)	0.20 (0.11, 0.43)	0.18 (0.12, 0.29)	0.12 (0.06, 0.24)
$\Psi \text{ CV}$	24%	45%	24%	53%	24%	35%	23%	34%
MRT ^e	0.8	35.0	0.8	35.9	0.8	36.0	0.8	29.3

^a Density (fishers 100 km^{-2}).

^b Baseline detectability for an individual whose activity centre is located precisely at the trap.

^c Spatial scale parameter.

^d Proportion of individuals from the data augmented population.

^e Model run time (hours).

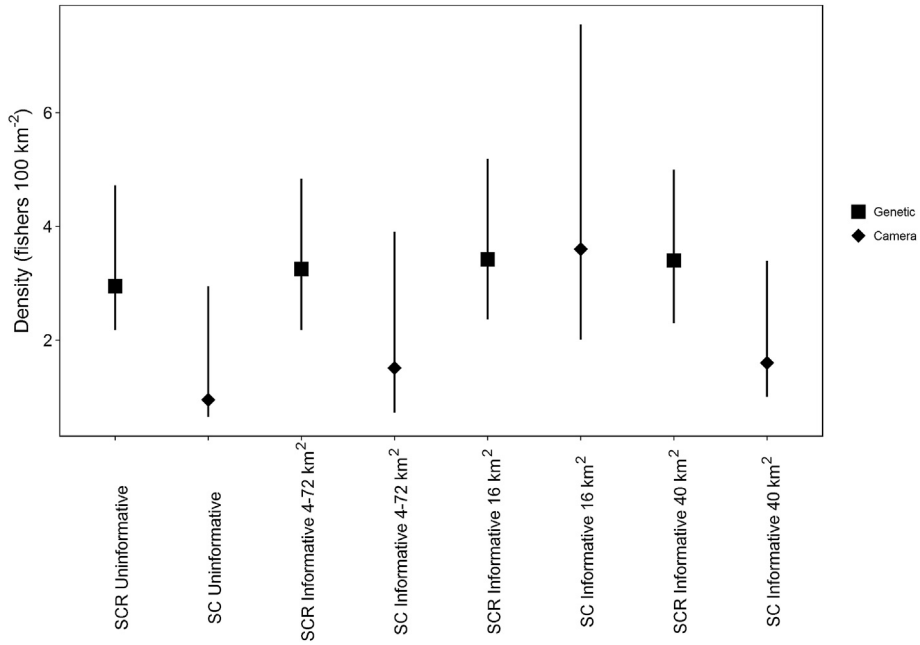


Fig. 2. Spatial capture-recapture (SCR; genetic survey) and spatial count (SC; camera survey) model fisher density estimates (mode \pm 95% Bayesian credible interval). Models varied by their σ prior, which was either uninformative or based on home range estimates varying between 4 and 72 km², or weighted at 16 km² and 40 km².

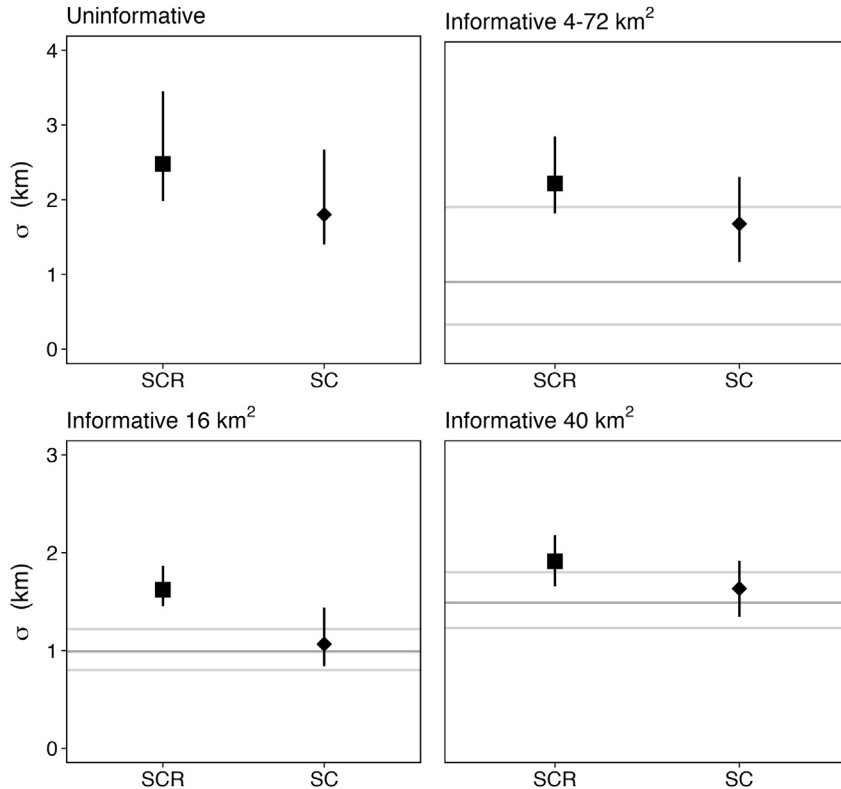


Fig. 3. Spatial capture-recapture (SCR; genetic survey) and spatial count (SC; camera survey) model fisher σ estimates (mode \pm 95% Bayesian credible interval). Models varied by their σ prior, which was either uninformative or based on home range estimates varying between 4 and 72 km², or weighted at 16 km² and 40 km². The horizontal lines depict the median (dark gray) and 2.5 and 97.5 quartiles (light gray) for the σ prior gamma distributions.

surveys and substantially less for camera trap surveys (Fig. D1). By the third survey, the cumulative cost of the camera trap survey was less than the genetic survey (Fig D1).

Because the 95% BCI were too large to be informative for the full SCR models, we ran simulations to determine the number of sampling occasions necessary to produce density estimates while including sex and trap-behaviour covariates. We based simulated parameters on output from the full SCR model and set K to 4, 8 and 12 (Appendix E). Simulation results indicated that tripling the number of sampling occasions ($K = 12$) produced 1.08 95% BCI widths on average, assuming a population density of 4.42 fishers 100 km^{-2} (Fig E1). Assuming that tripling the number of occasions would also triple the number of samples—and considering only cost increases to field labour and DNA processing—a genetic survey with 12 sampling occasions would cost \$75 746, which is comparable to the cost of our camera trap survey.

4. Discussion

This examination of SCR and SC density estimates of a recovering mesocarnivore illustrates that camera trap data from unmarked individuals have the potential to inform species conservation research and management, with careful interpretation. The SC model, fit using camera trap data, slightly underestimated density relative to the SCR model [1.51 (0.73–3.91 95% BCI) fishers 100 km^{-2}] compared to the base SCR model, fit using genetic data [3.25 (2.18–4.84 95% BCI) fishers 100 km^{-2}]. The SCR and SC model BCIs overlapped and were of similar widths, indicating that the SC model estimates were plausible, albeit less precise—21% CV for the SCR model compared to 52% CV for the SC model—and must be interpreted cautiously. Despite the relative imprecision, the SC density estimate precision was comparable to or better than the precision from SC density estimates of other carnivores (Jiménez et al., 2017; Kane et al., 2015). Genetic surveys were only more cost-effective than camera trap surveys if genetic sampling occasions were kept to a minimum and cameras were used only once. Density estimates from complex SCR models, those that include sex and trap-behaviour covariates, would require increased genetic sampling and associated costs. In our study, modelling the density of unmarked fishers detected from camera trap surveys produced density estimates that could be cautiously used as a population estimate, potentially augmented with other sampling methods in a long-term conservation monitoring program.

Fisher densities estimated from the SC models were dependent on the choice of σ priors, which generally approximated the range of reported fisher home range estimates (Arthur et al., 1989; Powell and Zielinski, 1994). In contrast, the σ prior influenced λ_0 for the SCR models, understandable given that in SCR models density is influenced both by σ and an individual's use of specific traps; thus constraining σ will cause λ_0 to fluctuate. There was a closer mirroring of posterior and prior σ distributions for the SC models, revealing the influence of prior knowledge when modelling with relatively sparse detection data. Indeed, previous simulation studies on SC models found that posterior distributions were highly skewed and posterior precision was low when sample sizes were small to moderate (Chandler and Royle, 2013). Thus, we advise against using strongly informative priors and instead recommend using a range of unweighted prior knowledge, such as in our case where we used an informative prior for home range estimates between 4 and 72 km^2 . If reasonable prior knowledge is not available, we recommend only using SC models if simulations suggest that sample sizes of detections are high enough to warrant use of uninformative priors.

Fisher density in the Cooking Lake Moraine was relatively low. Density estimates were similar to estimates for a population in the sub-boreal spruce region of British Columbia, derived from minimum count alive and telemetry data (Weir and Corbould, 2006) and lower than estimates for populations in eastern North America (Furnas et al., 2017; Koen et al., 2007; Linden et al., 2017). In our study, average trap spacing was 2.8 km for the 64 sites, less than the recommended maximum of 2 σ average trap spacing (Efford and Fewster, 2013; Sollmann et al., 2012; Sun et al., 2014), suggesting trap spacing was appropriate in our study for either sampling method. Back-transforming σ estimates yielded larger than expected home range sizes, particularly for the SCR model. This is likely due to the fact that camera traps detected fishers more readily than the genetic sampling; similar to multi-method studies elsewhere (Clare et al., 2017; Fisher et al., 2016; Fisher and Bradbury, 2014), nearly half the sites with camera detections did not produce genetic detections, either because there was no genetic sample or individual identity of the genetic sample was not successful. While useful for assessing the adequacy of the sampling design we caution against using σ estimates to infer fisher home range size, particularly when sample sizes are low and spatial recaptures are limited.

In contrast, we consider λ_0 estimates as appropriate, due to the relatively narrow BCIs and comparability between methods. We used baited traps, as fishers in our study system occurred at low densities, and baiting is likely necessary to ensure adequate numbers of detections for modelling (du Preez et al., 2014; Gerber et al., 2012). When carnivores occur in low densities and traps are not baited, SCR densities estimates can be very imprecise (e.g., Sunarto et al., 2013). Given that mustelids are more likely to visit a trap if they have visited it previously (Linden et al., 2017; e.g., Royle et al., 2011; Sirén et al., 2016), we had hoped to include a trap-behaviour covariate in the SCR model. Unfortunately, despite using a Bayesian approach, the low sample size inhibited inclusion of covariates. Therefore we recommend future genetic surveys increase the sampling occasions from 1 to 3 per month, for a total of 12 over the study period. For other studies we highly recommend simulating data, using parameters derived either from a pilot study or local knowledge, to ensure sufficient genetic sampling occasions.

While the SC models show promise in our study, there may be conditions under which they are not appropriate, such as estimating density of rarer and more elusive species with very low detection rates. In addition, when sampling units are not set up in a grid array, SC models are unlikely to converge (Sollmann et al., 2013), or they might produce estimates too

imprecise to be useful (Kane et al., 2015). We therefore suggest that future simulation and empirical studies test the sensitivity of SC models to trap configuration (e.g., Sun et al., 2014). Improvement in model convergence and precision may be gained through emerging approaches that incorporate additional information about the population, such as partially marked individuals and/or space usage from telemetry data (Augustine et al., 2016; Gopalaswamy et al., 2012; Sollmann et al., 2013).

Similar to other studies, we found that camera trap surveys can be as cost-effective as other sampling methods (Cheng et al., 2017; Sirén et al., 2016), or relatively inexpensive when re-using cameras over multiple surveys. As camera traps sample multiple species, estimating density for multiple species would only incur additional costs of statistical analysis, as opposed to genetic surveys, which would incur costs of analysing genetic markers for each species. If physiological, genetic, individual, or population dynamics are driving a species-specific monitoring program, information gleaned from genetic surveys are invaluable (Diefenbach et al., 2015; Murphy et al., 2016). If community dynamics or multi-species density estimates are the priority, the initial start-up costs of a camera trap survey are greatly outweighed by the ability to survey multiple species concurrently (although we note that trade-offs likely exist in sampling design across species with different densities and movement behaviours, cf. Neilson et al., 2018). SCR studies of species of conservation concern predominantly use camera trap data to estimate density—these data could conceivably be mined to estimate densities of non-target species (e.g., Rayan et al., 2012; Sollmann et al., 2014). The use of genetic surveys, camera trap surveys, or integrating both (e.g., Chandler and Clark, 2014) comes down to the research questions of interest and funding constraints.

The nature of remotely operating cameras—where researchers can post hoc discretize continuous data into desired survey durations—compared to hair traps—where frequency of sampling occasion is limited by field costs, logistics, and DNA degradation in the field (Kendall and Mckelvey, 2008)—means that camera trap surveys can require fewer field visits, but produce richer detection datasets, than genetic surveys. Thus, camera trap surveys for density estimation are more likely to be cost-effective in terms of human resources over the short-term and actual dollars over the long-term, particularly when genetic sampling is sufficiently high-frequency to generate data for sex and trap-behaviour SCR models and for successful DNA identification. Most camera trap studies of unmarked populations have relied on proxies of density, such as relative abundance indices (detection rates) or occupancy (Burton et al., 2015). Such indices can be problematic as they confound density and movement (Neilson and Boutin, 2017; Parsons et al., 2017) and direct estimates of density are preferable. Where multi-species density estimation is not the primary goal, we concur with other studies that suggest a meld of methods is the optimal approach for long-term monitoring (e.g., Chandler and Clark, 2014): for example, by integrating infrequent extensive genetic sampling surveys with unmarked camera trap survey density estimation. The multi-species capacity and finer temporal resolution of camera trap data can aid ecological inquiry by yielding information about community processes that can affect species density, such as the timing and duration of interactions with predators and competitors (Frey et al., 2017), and behavioural patterns (Caravaggi et al., 2017). With the wealth of camera trap data now available to researchers, SC models may provide baseline density estimates for populations otherwise not monitored, which can be used as a core component in monitoring programs augmented with other methods.

Data accessibility

Data associated with this manuscript are available from the Dryad Digital Repository: [doi:10.5061/dryad.dh7cd36](https://doi.org/10.5061/dryad.dh7cd36).

Acknowledgements

Funding for this project was provided by InnoTech Alberta grants to ACB and JTF; Government of Alberta (Environment and Parks), The Beaver Hills Initiative, Alberta Conservation Association grants to JTF; and NSERC (Canada), Royal Canadian Geographic Society, TD Friends of the Environment Foundation, and the Fur Institute of Canada scholarships to FECS. We thank M. Pybus, G. Hood, D. Vujnovic, and B. Eaton, for help with project oversight and design and field logistics, and M. McAdie, I. Brusselers, T. Zembal, S. Frey, N. Heim, and S. Murray for help with data collection. Research was permitted by Alberta Environment and Parks (16-004) and University of Alberta Animal Care Committee (AUP00000518).

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2018.e00411>.

References

- Arthur, S.M., Krohn, W.B., Gilbert, J.R., 1989. Home range characteristics of adult Fishers. *J. Wildl. Manag.* 53, 674. <https://doi.org/10.2307/3809196>.
- Augustine, B., Royle, J.A., Kelly, M., Satter, C., Alonso, R., Boydston, E., Crooks, K., 2016. Spatial Capture-recapture with Partial Identity: an Application to Camera Traps. <https://doi.org/10.1101/056804> bioRxiv.
- Avgan, B., Zimmermann, F., Güntert, M., Arkan, F., Breitenmoser, U., 2014. The first density estimation of an isolated Eurasian Lynx population in Southwest Asia. *Wildl. Biol.* 20, 217–221. <https://doi.org/10.2981/wlb.00025>.
- Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L.T.B., Macdonald, D.W., Packer, C., 2015. Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci. Unit. States Am.* 112, 14894–14899. <https://doi.org/10.1073/pnas.1500664112>.
- Borchers, D.L., Efford, M.G., 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64, 377–385. <https://doi.org/10.1111/j.1541-0420.2007.00927.x>.

- Bradley, D., Conklin, E., Papastamatiou, Y.P., McCauley, D.J., Pollock, K., Pollock, A., Kendall, B.E., Gaines, S.D., Caselle, J.E., 2017. Resetting predator baselines in coral reef ecosystems. *Sci. Rep.* 7, 43131. <https://doi.org/10.1038/srep43131>.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph Stat.* 7, 434. <https://doi.org/10.2307/1390675>.
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52, 675–685. <https://doi.org/10.1111/1365-2664.12432>.
- Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. *Remote Sens. Ecol. Conserv.* 3, 109–122. <https://doi.org/10.1002/rse2.48>.
- Chandler, R.B., Clark, J.D., 2014. Spatially explicit integrated population models. *Methods Ecol. Evol.* 5, 1351–1360. <https://doi.org/10.1111/2041-210X.12153>.
- Chandler, R.B., Royle, J.A.A., 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *Ann. Appl. Stat.* 7, 936–954. <https://doi.org/10.1214/12-AOAS610>.
- Cheng, E., Hodges, K.E., Sollmann, R., Mills, L.S., 2017. Genetic sampling for estimating density of common species. *Ecol. Evol.* <https://doi.org/10.1002/ece3.3137>.
- Clare, J., McKinney, S.T., DePue, J.E., Loftin, C.S., 2017. Pairing field methods to improve inference in wildlife surveys while accommodating detection covariance. *Ecol. Appl.* <https://doi.org/10.1002/eap.1587>.
- Dawson, D.K., Efford, M.G., 2009. Bird population density estimated from acoustic signals. *J. Appl. Ecol.* 46, 1201–1209. <https://doi.org/10.1111/j.1365-2664.2009.01731.x>.
- Diefenbach, D., Hansen, L., Bohling, J., Miller-Butterworth, C., 2015. Population and genetic outcomes 20 years after reintroducing bobcats (*Lynx rufus*) to Cumberland Island, Georgia USA. *Ecol. Evol.* 5, 4885–4895. <https://doi.org/10.1002/ece3.1750>.
- du Preez, B.D., Loveridge, A.J., Macdonald, D.W., 2014. To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biol. Conserv.* 176, 153–161. <https://doi.org/10.1016/j.biocon.2014.05.021>.
- Efford, M., 2004. Density estimation in live-trapping studies. *Oikos* 106, 598–610. <https://doi.org/10.1111/j.0030-1299.2004.13043.x>.
- Efford, M.G., Fewster, R.M., 2013. Estimating population size by spatially explicit capture-recapture. *Oikos* 122, 918–928. <https://doi.org/10.1111/j.1600-0706.2012.20440.x>.
- Evans, M.J., Rittenhouse, T.A.G., Hawley, J.E., Rego, P.W., 2017. Black bear recolonization patterns in a human-dominated landscape vary based on housing: new insights from spatially explicit density models. *Landscape Urban Plann.* 162, 13–24. <https://doi.org/10.1016/j.landurbplan.2017.01.009>.
- Fisher, J.T., Bradbury, S., 2014. A multi-method hierarchical modeling approach to quantifying bias in occupancy from noninvasive genetic tagging studies. *J. Wildl. Manag.* 78, 1087–1095. <https://doi.org/10.1002/jwmg.750>.
- Fisher, J.T., Heim, N., Code, S., Paczkowski, J., 2016. Grizzly bear noninvasive genetic tagging surveys: estimating the magnitude of missed detections. *PLoS One* 11, 1–16. <https://doi.org/10.1371/journal.pone.0161055>.
- Foran, D.R., Minta, S.C., Heinemeyer, K.S., 1997. DNA-based analysis of hair to identify species and individuals for population research and monitoring. *Wildl. Soc. Bull.* 25, 840–847.
- Frey, S., Fisher, J.T., Burton, A.C., Volpe, J.P., 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens. Ecol. Conserv.* 1–10. <https://doi.org/10.1002/rse2.60>.
- Fuller, T.K., York, E.C., Powell, S.M., Decker, T. a., DeGraaf, R.M., 2001. An evaluation of territory mapping to estimate Fisher density. *Can. J. Zool.* 79, 1691–1696. <https://doi.org/10.1139/z01-129>.
- Furnas, B.J., Landers, R.H., Callas, R.L., Matthews, S.M., 2017. Estimating population size of Fishers (*Pekania pennanti*) using camera stations and auxiliary data on home range size. *Ecosphere* 8, e01747. <https://doi.org/10.1002/ecs2.1747>.
- Gardner, B., Royle, J.A., Wegan, M.T., Rainbolt, R.E., Curtis, P.D., 2010. Estimating black bear density using DNA data from hair snares. *J. Wildl. Manag.* 74, 318–325. <https://doi.org/10.2193/2009-101>.
- Gerber, B.D., Karpanty, S.M., Kelly, M.J., 2012. Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Popul. Ecol.* 54, 43–54. <https://doi.org/10.1007/s10144-011-0276-3>.
- Gopalaswamy, A.M., Royle, J.A., Delampady, M., Nichols, J.D., Karanth, K.U., Macdonald, D.W., 2012. Density estimation in tiger populations: combining information for strong inference. *Ecology* 93, 1741–1751. <https://doi.org/10.1890/11-2110.1>.
- Jiménez, J., Nuñez-Arjona, J.C., Rueda, C., González, L.M., García-Domínguez, F., Muñoz-Igualada, J., López-Bao, J.V., 2017. Estimating carnivore community structures. *Sci. Rep.* 7, 41036. <https://doi.org/10.1038/srep41036>.
- Kachel, S.M., McCarthy, K.P., McCarthy, T.M., Oshurmamadov, N., 2016. Investigating the potential impact of trophy hunting of wild ungulates on snow leopard *Panthera uncia* conservation in Tajikistan. *Oryx* 48, 1–8. <https://doi.org/10.1017/S0030605316000193>.
- Kane, M.D., Morin, D.J., Kelly, M.J., 2015. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (*Panthera leo*). *Biodivers. Conserv.* 24, 3527–3541. <https://doi.org/10.1007/s10531-015-1012-7>.
- Kellner, K., 2016. jagsUI: a Wrapper Around “rjags” to Streamline “JAGS” Analyses.
- Kendall, K., Mckelvey, K., 2008. Hair collection. In: Long, R., MacKay, P., Zielinski, W., Ray, J. (Eds.), *Noninvasive Survey Methods for Carnivores*. Island Press, Washington, pp. 135–176.
- Koen, E.L., Bowman, J., Findlay, C.S., Zheng, L., 2007. Home range and population density of Fishers in eastern Ontario. *J. Wildl. Manag.* 71, 1484–1493. <https://doi.org/10.2193/2006-133>.
- Linden, D.W., Fuller, A.K., Royle, J.A., Hare, M.P., 2017. Examining the occupancy-density relationship for a low-density carnivore. *J. Appl. Ecol.* 54, 2043–2052. <https://doi.org/10.1111/1365-2664.12883>.
- Mcgregor, H.W., Legge, S., Potts, J., Jones, M.E., Johnson, C.N., 2015. Density and home range of feral cats in north-western Australia. *Wildl. Res.* 42, 223–231. <https://doi.org/10.1071/WR14180>.
- Mollet, P., Kéry, M., Gardner, B., Pasinelli, G., Royle, J.A., 2015. Estimating population size for capercaillie (*Tetrao urogallus* L.) with spatial capture-recapture models based on genotypes from one field sample. *PLoS One* 10, e0129020. <https://doi.org/10.1371/journal.pone.0129020>.
- Muñoz, D.J., Miller, D.A.W., Sutherland, C., Grant, E.H.C., 2016. Using spatial capture–recapture to elucidate population processes and space-use in herpetological studies. *J. Herpetol.* 50, 570–581. <https://doi.org/10.1670/15-166>.
- Murphy, S.M., Cox, J.J., Augustine, B.C., Hast, J.T., Guthrie, J.M., Wright, J., McDermott, J., Maehr, S.C., Plaxico, J.H., 2016. Characterizing recolonization by a reintroduced bear population using genetic spatial capture–recapture. *J. Wildl. Manag.* 80, 1390–1407. <https://doi.org/10.1002/jwmg.21144>.
- Neilson, E.W., Avgar, T., Burton, A.C., Broadley, K., Boutin, S., 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere* 9. <https://doi.org/10.1002/ecs2.2092> e02092–n/a.
- Neilson, E.W., Boutin, S., 2017. Human disturbance alters the predation rate of moose in the Athabasca oil sands. *Ecosphere* 8, e01913. <https://doi.org/10.1002/ecs2.1913>.
- Newey, S., Davidson, P., Nazir, S., Fairhurst, G., Verdicchio, F., Irvine, R.J., van der Wal, R., 2015. Limitations of recreational camera traps for wildlife management and conservation research: a practitioner’s perspective. *Ambio* 44, 624–635. <https://doi.org/10.1007/s13280-015-0713-1>.
- Parsons, A.W., Forrester, T., McShea, W.J., Baker-Whattom, M.C., Millsbaugh, J.J., Kays, R., 2017. Do occupancy or detection rates from camera traps reflect deer density? *J. Mammal.* 98, 1547–1557. <https://doi.org/10.1093/jmammal/gyx128>.
- Plummer, M., 2016. Rjags: Bayesian Graphical Models Using MCMC.
- Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proc. 3rd Int. Work. Distrib. Stat. Comput. (DSC 2003)*, pp. 20–22. doi:10.1.1.13.3406.
- Plummer, M., Best, N., Cowles, K., Vines, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. *R. News* 6, 7–11.
- Powell, R.A., 1982. *The fisher: Life History, Ecology and Behavior*. University of Minnesota Press.

- Powell, R.A., Zielinski, W.J., 1994. Fisher. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J. (Eds.), *American Marten, Fisher, Lynx, and Wolverine in Western United States*. United States Forest Service, General Technical Reports RM-254, pp. 38–73.
- Rayan, D.M., Mohamad, S.W., Dorward, L., Aziz, S.A., Clements, G.R., Christopher, W.C.T., Traeholt, C., Magintan, D., 2012. Estimating the population density of the Asian tapir (*Tapirus indicus*) in a selectively logged forest in Peninsular Malaysia. *Integr. Zool.* 7, 373–380. <https://doi.org/10.1111/j.1749-4877.2012.00321.x>.
- Rich, L.N., Kelly, M.J., Sollmann, R., Noss, A.J., Maffei, L., Arispe, R.L., Paviolo, A., De Angelo, C.D., Di Blanco, Y.E., Di Bitetti, M.S., 2014. Comparing capture–recapture, mark–resight, and spatial mark–resight models for estimating puma densities via camera traps. *J. Mammal.* 95, 382–391. <https://doi.org/10.1644/13-MAMM-A-126>.
- Royle, J.A., 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60, 108–115. <https://doi.org/10.1111/j.0006-341X.2004.00142.x>.
- Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2014. *Spatial Capture-recapture*, 1st Ed, *Spatial Capture-recapture*. Elsevier, Oxford. <https://doi.org/10.1016/B978-0-12-405939-9.00020-7>.
- Royle, J.A., Dorazio, R.M., 2012. Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. *J. Ornithol.* 152, 521–537. <https://doi.org/10.1007/s10336-010-0619-4>.
- Royle, J.A., Magoun, A.J., Gardner, B., Valkenburg, P., Lowell, R.E., 2011. Density estimation in a wolverine population using spatial capture–recapture models. *J. Wildl. Manag.* 75, 604–611. <https://doi.org/10.1002/jwmg.79>.
- Royle, J.A., Young, K.V., 2008. A hierarchical model for spatial capture–recapture data. *Ecology* 89, 2281–2289. <https://doi.org/10.1890/07-0601.1>.
- Scotson, L., Fredriksson, G., Ngoprasert, D., Wong, W.-M., Fieberg, J., 2017. Projecting range-wide sun bear population trends using tree cover and camera-trap bycatch data. *PLoS One* 12, e0185336. <https://doi.org/10.1371/journal.pone.0185336>.
- Sirén, A., Pekins, P., Abdu, P., Ducey, M., 2016. Identification and density estimation of american martens (*Martes americana*) using a novel camera-trap method. *Diversity* 8, 3. <https://doi.org/10.3390/d8010003>.
- Sollmann, R., Gardner, B., Belant, J.L., 2012. How does spatial study design influence density estimates from spatial capture–recapture models? *PLoS One* 7, e34575. <https://doi.org/10.1371/journal.pone.0034575>.
- Sollmann, R., Gardner, B., Parsons, A.W., Stocking, J.J., McClintock, B.T., Simons, T.R., Pollock, K.H., O'Connell, A.F., 2013. A spatial mark–resight model augmented with telemetry data. *Ecology* 94, 553–559. <https://doi.org/10.1890/12-1256.1>.
- Sollmann, R., Linkie, M., Haidir, I. a, Macdonald, D.W., 2014. Bringing clarity to the clouded leopard *Neofelis diardi*: first density estimates from Sumatra. *Oryx* 48, 536–539. <https://doi.org/10.1017/S003060531400043X>.
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Front. Ecol. Environ.* 15, 26–34. <https://doi.org/10.1002/fee.1448>.
- Stewart, F.E.C., Fisher, J.T., Burton, A.C., Volpe, J.P., 2018. Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere* 9, e02112. <https://doi.org/10.1002/ecs2.2112>.
- Stewart, F.E.C., Volpe, J.P., Taylor, J.S., Bowman, J., Thomas, P.J., Pybus, M.J., Fisher, J.T., 2017. Distinguishing reintroduction from recolonization with genetic testing. *Biol. Conserv.* 214, 242–249. <https://doi.org/10.1016/j.biocon.2017.08.004>.
- Sun, C.C., Fuller, A.K., Royle, J.A., 2014. Trap configuration and spacing influences parameter estimates in spatial capture–recapture models. *PLoS One* 9, e88025. <https://doi.org/10.1371/journal.pone.0088025>.
- Sunarto, Kelly M.J., Klenzendorf, S., Vaughan, M.R., Zulfahmi, Hutajulu M.B., Parakkasi, K., 2013. Threatened predator on the equator: multi-point abundance estimates of the tiger *Panthera tigris* in central Sumatra. *Oryx* 47, 211–220. <https://doi.org/10.1017/S0030605311001530>.
- Tobler, M.W., Powell, G.V.N., 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biol. Conserv.* 159, 109–118. <https://doi.org/10.1016/j.biocon.2012.12.009>.
- Torres-Vila, L.M., Sanchez-González, Á., Ponce-Escudero, F., Martín-Vertedor, D., Ferrero-García, J.J., 2012. Assessing mass trapping efficiency and population density of *Cerambyx welensii* Küster by mark–recapture in dehesa open woodlands. *Eur. J. For. Res.* 131, 1103–1116. <https://doi.org/10.1007/s10342-011-0579-0>.
- Weir, R.D., Corbould, F.B., 2006. Density of Fishers in the sub-boreal spruce biogeoclimatic zone of British Columbia. *Northwest. Nat.* 87, 118–127. [https://doi.org/10.1898/1051-1733\(2006\)87\[118:DOFITS\]2.0.CO;2](https://doi.org/10.1898/1051-1733(2006)87[118:DOFITS]2.0.CO;2).
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and Management of Animal Populations*. Academic Press.